ECOLOGICAL STUDIES ON TWO UNATTACHED CORALLINE ALGAE FROM WESTERN IRELAND

by DANIEL W. J. BOSENCE

ABSTRACT. Two free-living coralline algae occur sublittorally in Mannin Bay, Connemara, Eire. Locally they form 30-cm high autochthonous banks which cover areas up to 1 sq km and have a diverse associated fauna. The algae are restricted by light to depths between 1 m and 16 m. Within this depth range the development of the banks is controlled by wave-induced currents and the algae are broken down to form an algal gravel which supports a poor fauna.

There is variation in growth form within the species and a scheme is suggested for describing morphology in free-living corallines. Shapes vary from spheroidal, ellipsoidal, to discoidal. Within these shape classes branching density varies. Densely branched forms are found in the exposed areas and open-branched forms in the quiet areas of the bay. Wave-tank studies suggest that densely branched forms are most easily transported. Dense branching develops as a response to rolling on the substrate which damages the growing apex. Following abrasion, lateral branches form within the thallus.

The palaeontological implications of the work are discussed and comparisons made with other algal bank deposits.

UNATTACHED coralline algae (subfamily Melobesioideae) can be important producers of carbonate sediment in the sublittoral zone where they form both autochthonous banks and transported algal gravels. These algal sediments are known from both tropical (Turmel and Swanson 1972) and temperate environments (Foslie 1894; Cabioch 1966, 1970; Adey and MacIntyre 1973) where they are referred to as maerl (Lemoine 1910).

These unattached algae differ from the epilithic crustose corallines in their morphology, reproduction, and ecology. The unattached forms live in soft substrate areas. Their morphology varies from open branched thalli to densely branched algal nodules (rhodoliths). Reproduction is by vegetative means and by spores which settle on carbonate or clastic grains. The epilithic corallines of temperate waters have been studied in some detail by Cabioch 1972 and refs. and Adey and Adey 1973 and refs. Although the morphology and systematics of unattached corallines have been described by Cabioch 1966 and Adey and McKibbin 1970 there is little information on their ecology and sedimentology (Adey and McKibbin 1970; Adey and Adey 1973).

The object of this paper is to describe and interpret the distribution of autochthonous banks formed by two unattached corallines, analyse the ecological factors responsible for the variation in growth form, and to discuss the palaeontological implications arising therefrom.

ENVIRONMENTAL SETTING AND LITHOFACIES

The bathymetry and location of Mannin Bay are shown in text-fig. 1. A submarine valley leads into the bay and up to a slope levelling off at about 8 m to form a platform with occasional rocky outcrops. The shore is mainly rocky (Dalradian metasediments) but some sandy carbonate beaches and dunes are present. In the sheltered lagoons a muddy shore is found.
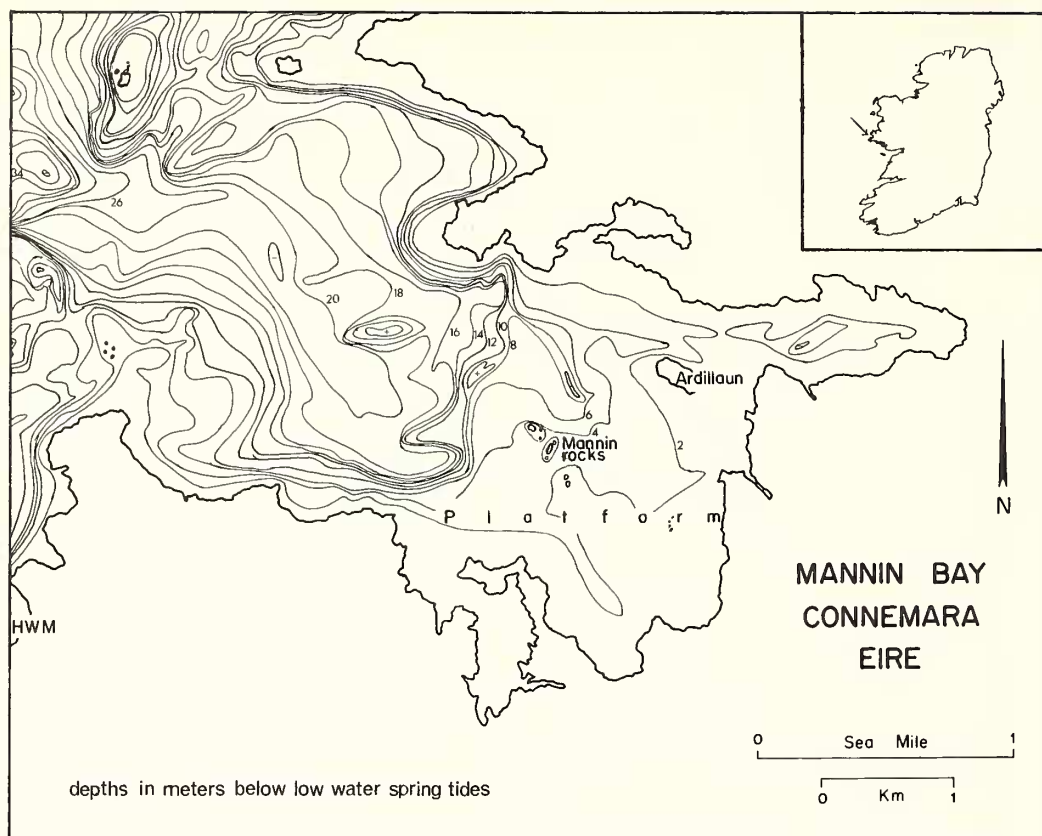
TEXT-FIG. 1. Location and bathymetry of Mannin Bay (after Buller 1969).

The sea-water is normal marine with seasonal water temperatures varying from a February mean minimum of 5 °C. to an August mean maximum of 15 °C. Salinity varies seasonally from 33·5 to 35°/$_{oo}$ (Lees *et al.* 1969).

The normal marine environment is the result of mixing by tidal currents which show a simple ebb-flood pattern with a superimposed rotary pattern in South Mannin Bay (text-fig. 2). The currents measured are not strong enough to transport the algal clasts (Buller 1969). Study of the gravel bed forms shows that the main hydraulic forces are oscillatory currents produced by waves.

The strongest and most frequent winds are from the south-west (Lees *et al.* 1969).

Lithofacies

The sediments of Mannin Bay are mainly carbonate as is the case with much of the littoral and sublittoral of the coast of western Eire (Keary 1969, 1970; Lees *et al.* 1969). The sediments of Mannin Bay can be divided into four major sedimentary facies (text-fig. 3) based on particle size, composition, and mineralogy of the carbonate grains (Buller 1969; Gunatilaka 1972).

Mud facies. Dark muds are found in the shallow and most sheltered parts of Mannin
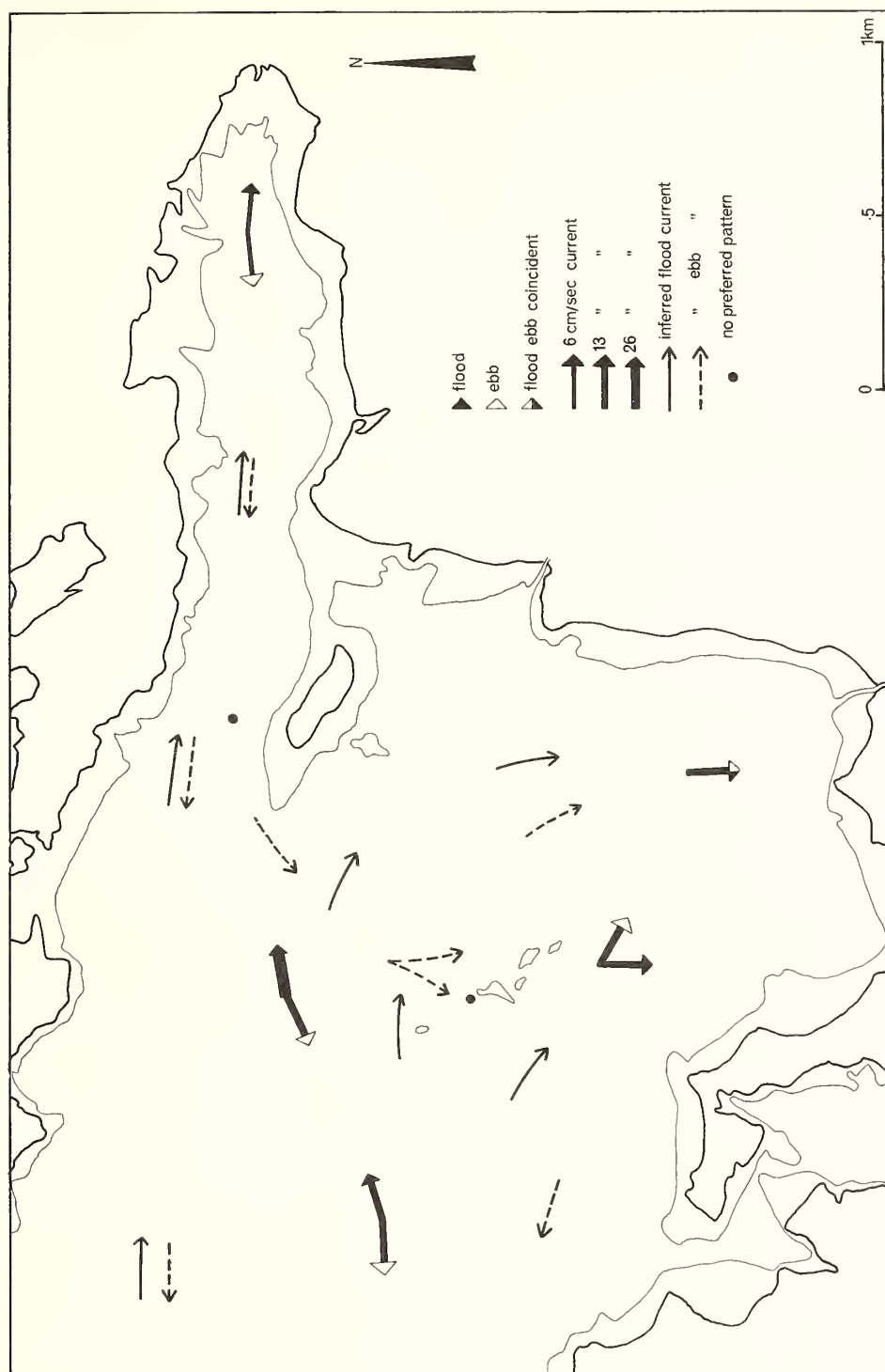
TEXT-FIG. 2. Direction and strength of tidal currents, Mannin Bay (after Buller 1969).
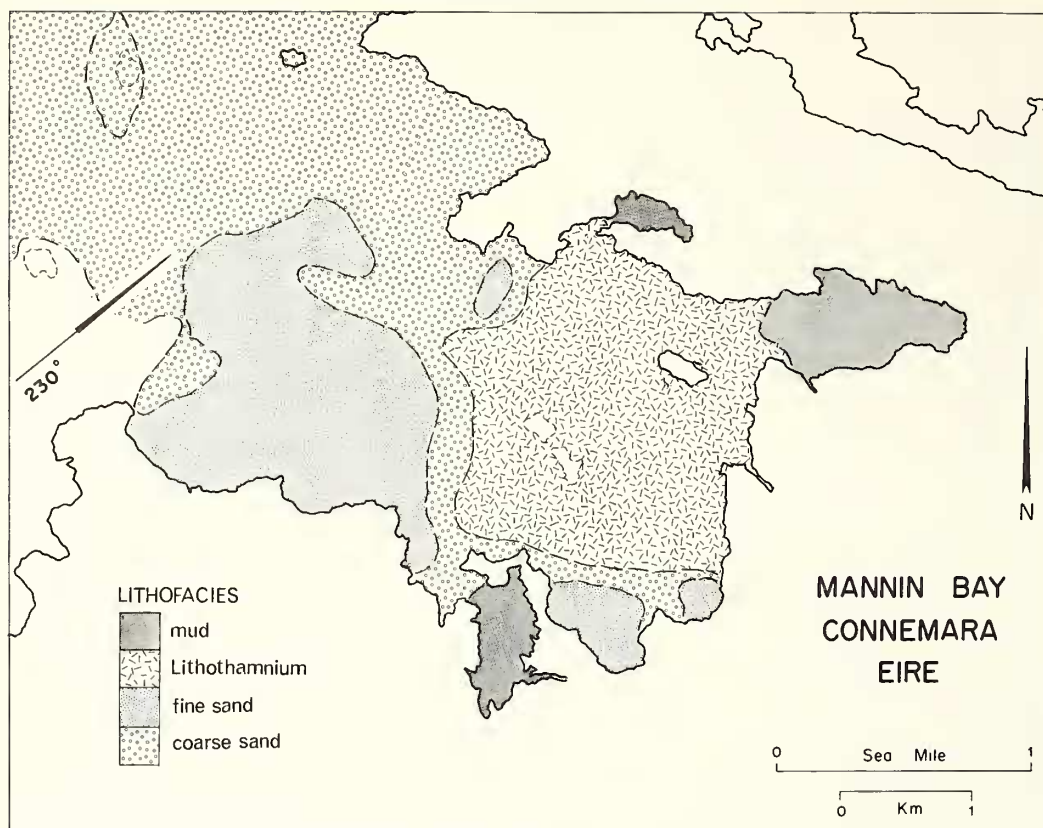
TEXT-FIG. 3. Lithofacies and input of hydraulic energy, Mannin Bay (after Buller 1969; Gunatilaka 1972).

Bay where currents are weak. The carbonate content of the muds rarely exceeds 40% (Gunatilaka 1972). Epiphytic filamentous algae are common in these quiet areas and they trap mud as they grow, so forming oncolites (Pl. 52, fig. 1).

Lithothamnium *facies.* This facies, the principal concern of this paper, covers the platform area of Mannin Bay and is composed of both living and dead unattached coralline algae (Pl. 52, figs. 4–6).

EXPLANATION OF PLATE 52

Fig. 1. Underwater photograph of filamentous algae epiphytic on *Lithothamnium corallioides* forming oncolites, ×1/6.

Fig. 2. Underwater photograph of fine-sand facies with bioturbated surface, ×1/20.

Fig. 3. Underwater photograph of coarse-sand facies with wave-formed ripples, ×1/20.

Fig. 4. Underwater photograph of wave-rippled algal gravel with dead infaunal bivalve shells in ripple troughs, ×1/20.

Fig. 5. Underwater photograph of surface of algal bank of *Phymatolithon calcareum* with *Asterias rubens*, ×1/4 (foreground).

Fig. 6. Core through algal bank. Note stacking of algal thalli and grain-supported sediment with micrite matrix at depth, ×0·5.

PLATE 52
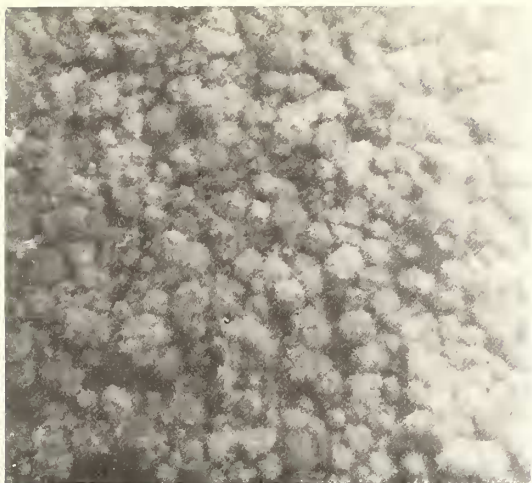
BOSENCE, coralline algae

Fine sand facies. This facies accumulates in the sheltered parts of the bays and is composed mainly of foraminifera, echinoderm, bryozoan, and ostracod debris (Pl. 52, fig. 2).

Coarse sand facies. The more open parts of the bay contain a very coarse sand or gravel composed of large proportions of *Mytilus edulis* and barnacle grains suggesting derivation from the offshore islands and 'reefs' (Pl. 52, fig. 3).

The distribution of the sedimentary facies can, in the main, be explained in terms of the input of hydraulic energy into the bay. The tidal, wind, and longest fetch directions indicate that the maximum energy is derived from about 230° N. (text-fig. 3). The area most exposed to this direction is represented by the coarse-sand facies. Where slight protection is afforded fine sand accumulates and in the very sheltered bay heads mud is deposited (Buller 1969). The *Lithothamnium* facies does not fit this pattern as it is basically an autochthonous deposit and the grain size is related to the size of the thallus and its comparative rate of destruction.

THE MAERL SPECIES

General

The *Lithothamnium* facies of Buller (1969) is composed of the unattached calcareous algae *L. corallioides* Crouan and *Phymatolithon calcareum* (Pallas) Adey and McKibbin. The living algae cover up to 100% of the sea-floor and live in both quiet and exposed environments within the depth range of extreme low-water spring tides to 16 m (text-figs. 1, 6). Where growth is prolific an autochthonous three-dimensional growth structure is formed by the algal thalli which may be stacked to a height of 30 cm and covering areas measured in thousands of square metres, so forming a bank (Pl. 52, figs. 5–6; text-fig. 6). These banks are semi-rigid structures formed by branches of neighbouring algal thalli intergrowing. The strength of the bank is enhanced by the binding effect of epiphytic soft-tissued algae (see also Cabioch 1969). Cores through the bank (Pl. 52, fig. 6) show the three-dimensional structure of the living algae. Mud is trapped by the network of algal thalli and by the algal mucilage so that with depth a muddy matrix is formed. This matrix gradually buries and kills the algae. Excavation through the bank with an air-lift suction sampler shows a similar structure to a depth of 1 m.

The banks are broken down locally by physical and biological erosion to form a gravel-sized bioclastic sediment (Pl. 52, fig. 4). This is either transported into symmetrical ripples by wave-induced oscillatory currents with a small amount of living maerl in the ripple troughs, or it is a bioturbated bottom.

Biology

The banks can consist of one or both maerl species in varying proportions and they support a complex biota. The main ecological groups are: phytophagous gastropods (which utilize the organic debris trapped by algal mucilage); boring polychaetes, algae, and bivalves (which use the alga as a hard carbonate substrate); infaunal deposit and suspension feeders; nestling ophiuroids, crustacea, polychaetes, and

bivalves; epifaunal attached bryozoa, serpulids, and sponges; vagile epifaunal verte-
brates, echinoderms, decapods, and other crustacea; epiphytic algae, including
filamentous red algae and red and brown macrophytes. The associated fauna has been
studied by Cabioch (1968) in Brittany and Keagan (1973) in Kilkieran and Galway
Bays, western Eire; the flora by Cabioch (1969) in Brittany.

The life cycles and morphogeneses of the maerl species have been recently described
by both Cabioch (1972) and Adey and McKibbin (1970) and their results are sum-
marized below and in text-fig. 4.

The main form of reproduction observed in Mannin Bay is vegetative. The thallus
is broken by strong bottom currents and by organic reworking of the maerl. The plants
only occasionally reproduce by the production of asexual spores. Sexual reproductive
bodies have not been described, although Cabioch (1970) illustrates a sexual con-
ceptacle of *P. calcareum*. The asexual spores are borne in conceptacles developed from
the perithallial meristem in *L. corallioides* and within the perithallium in *P. calcareum*.
Their development is shown in text-fig. 4.

The branches of the thallus are of multiaxial or 'fountain' construction with fila-
ments of unlimited growth forming a central medulla (secondary hypothallus of
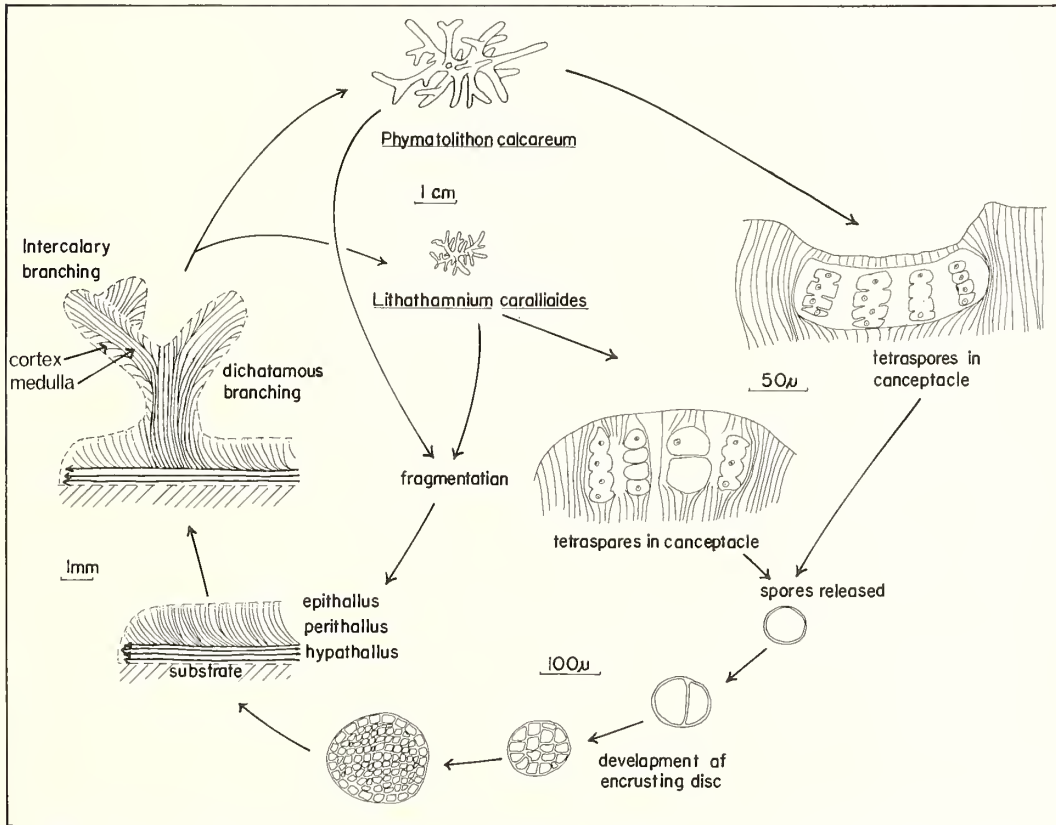
TEXT-FIG. 4. Life cycles and morphogeneses of *Phymatolithon calcareum* and *Lithothamnium corallioides*
(after Cabioch 1972; Adey and McKibbin 1973).

Cabioch 1972). These axial filaments branch and grow laterally as filaments of limited growth forming a cortex with a width typical for the species.

Growth is periodic as illustrated by layers of different cell size. These growth layers cover the apex and some way down each branch (Pl. 53, fig. 1). The growth layers and filaments illustrate that growth may be patchy and occasionally abrasion and rehealing can be found (Pl. 53, figs. 15–16).

Branching occurs in two different ways. In dichotomous branching the axial filaments diverge to form two equal branches with a plane of symmetry between them (Pl. 53, fig. 1). Intercalary branching occurs through rejuvenation of the lateral filaments. This is recognized by the initiation of new medulla from pre-existing lateral filaments (cortex) (Pl. 53, fig. 2) resulting from rejuvenation of the intercalary meristem, and so contrasting with dichotomous branching, which involves divergence of two parts of the apical meristem.

When the original sedimentary grain is covered and the branches form and rebranch the characteristic free-living growth forms are produced from the original encrusting stage.

Both the cortex and the medulla can be regenerated after breakage. Similarly old conceptacles can be filled and overgrown by new perithallium.

The relative importance of the two methods of asexual reproduction over a long period of time is not known but observations in the Baie de Morlaix by Cabioch (1969) show that the formation of conceptacles is very infrequent (about every 4–6 years).

Distribution

Seventy-three stations were dived on during the months of May–August 1972. At each station notes were taken on a perspex sheet and the percentage cover of the living maerl was estimated using a 50-cm quadrat. Live specimens are easily identified by their red colour. When dead, the thallus turns to a white or creamy brown colour. Most stations were photographed in colour using a Nikonos camera. A sample 10×20 cm and 10 cm deep was taken with a shovel and placed directly into a polythene bag. At the surface it was transferred to 10% neutralized formalin. When the sample was sorted the live algal material was stored in formalcohol.

Text-fig. 6 shows the percentage cover of living maerl in Mannin Bay. The distribution is discontinuous and three main concentrations (banks) can be noted: a northern central area, a central eastern area, and a small southern area. This distribution is discussed below with respect to the physical and chemical parameters operating in the bay.

The living maerl species occur from extreme Low Water Spring tidal level to a maximum depth of about 16 m but dense growth is not recorded below 8 m or above 1 m below Low Water Spring tides. This depth is somewhat shallower than the 7- and 25-m depth range found in Brittany by Lemoine (1910) and Cabioch (1970). Many environmental factors may change with depth of water. I now discuss which of these may be important in determining the distribution of the maerl species in Mannin Bay.

The salinity of the sea-water in the bay is normal marine and does not vary at one point of time. This cannot therefore be of importance to the distribution of the maerl species. This agrees with the work of Cabioch (1969) in the Baie de Morlaix in Brittany.

Experimental work by Adey and McKibbin (1970) suggests that low salinity may reduce growth rates.

Nutrient distribution has not been studied but the analyses for salinity, Ca, Mg, and pH indicate a very well mixed open marine environment and in the absence of any large streams or rivers bringing in concentrated nutrients there are not likely to be any areas of nutrient enrichment.

The availability of O_2 and CO_2 reflected in the Eh is not limiting as this is constantly positive (Gunatilaka 1972).

Grazers on the algae are unimportant. Although abundant, gastropods only brush the surface mucous and debris. There is no grazing by echinoids.

Although within the *Laminaria* Zone, there is no competition between the maerl species and these brown algae. The laminarians are restricted to hard substrate areas and the maerl species to the soft substrate areas of the bay. However, epiphytic filamentous algae cover the living maerl in quiet waters. In addition to this the filamentous algae trap mud and eventually smother the coralline algae to form oncolites (Pl. 52, fig. 1) thereby limiting the growth of the corallines.

The combined effects of temperature and light on the distribution of boreal and sub-arctic corallines has been studied both in the field and experimentally by Adey 1966, 1970, Adey and McKibbin 1970, and Adey and Adey 1973. Adey (1970) concludes that temperature and light control on growth are the major factors determining both depth distribution and geographic distribution of crustose and unattached corallines. The distribution of many corallines can be mapped into well-defined depth and latitudinal zones. However, an important problem is establishing the separate effects of light and temperature which both decrease with depth and may vary together with respect to latitude. This problem was overcome by Adey (1966) by plotting abundance data as a function of both depth and temperature and through experimental work which supports the correlations found in the field (Adey 1970). Most species show a combined effect but some show a depth distribution controlled by light and others are controlled by temperature.

Experimental work by Adey and McKibbin (1970) indicates maximum growth rate at 12–13 °C. for *Phymatolithon calcareum* and 10–12 °C. for *Lithothamnium corallioides* and very little growth at 170 lux at these temperatures. The luminosity for maximum growth was not established. Field measurements showed a maximum growth in the summer months for both species. The maerl species are distributed from the Mediterranean to Norway and, therefore, are well within their latitudinal range in western Eire.

I now compare these results and observations with the distribution of the maerl species in Mannin Bay where the summer mean bottom temperature varies from 11·75 °C. at 22 m to 13·5 °C. at 1·8 m (Scott 1970). If temperature were the overriding factor living maerl should be abundant within this depth range as it is in the temperature zone for maximum growth and the substrate, lack of mud sedimentation, and water currents appear to be suitable.

However, within this depth range growth is only found from extreme low-water springs to about 16 m and dense growth between depths of 1 and 8 m. This suggests that temperature is not the primary factor limiting depth in Mannin Bay although it is probably important on a larger geographic scale (Adey and Adey 1973) and may

be the cause of the lower depths recorded by Lemoine (1910) and Cabioch (1970) for Brittany.

The cut-off of surface irradiance in Mannin Bay by the sea was measured throughout the summer (1972) at various depths, conditions of turbidity, and surface roughness. This was measured just above the water surface and on the sea-bed with a calibrated light meter in a waterproof case. The effect water has on the different wavelengths was not measured as the absorption spectra of the maerl species is not known. Text-fig. 5 shows the measurements expressed as the percentage of surface
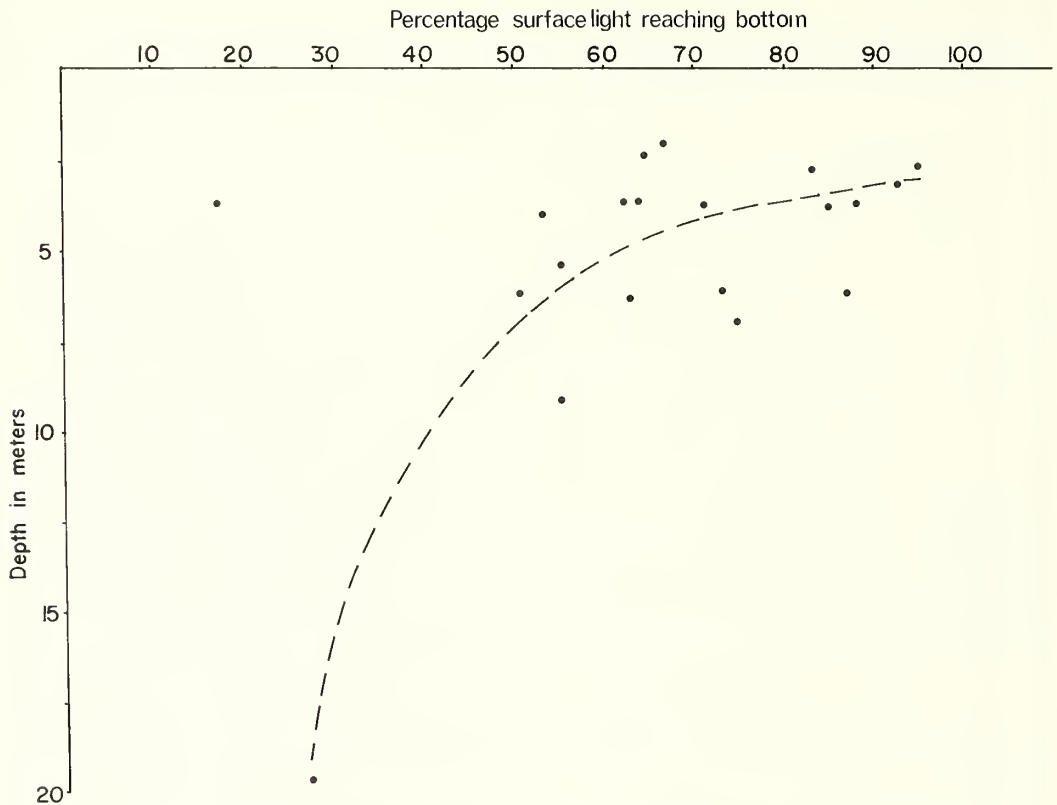
TEXT-FIG. 5. Graph illustrating cut-off of surface luminosity with depth, Mannin Bay.

luminosity (lux) reaching the bottom. The graph shows a rapidly decreasing penetration of light with depth and at the maximum depth at which the algae are found only about 30% of the surface light is reaching the sea-bed.

The values of luminosity measured within the depth range of 1–8 m vary from 160 to 1760 lux depending on ambient surface light, surface roughness, and turbidity. Therefore even at these shallow depths the luminosity is occasionally reaching the lowest values for growth recorded by Adey and McKibbin (1970).

The parameter used for estimating the relative bottom-current velocities was the presence or absence of wave-ripple marks. This has been noted for about seventy

stations during May–August 1972 and if present their orientation has been recorded with an underwater compass (text-fig. 7).

From wave theory (Barber 1965; Allen 1970) and experimental work (Bagnold 1947; Putnam and Johnson 1949) I interpret the distribution of wave ripples as follows. When deep-water waves enter the bay they only rarely have sufficient power to move sediment. I have occasionally found wave ripples (λ65 cm, H 5 cm) developed after storms on a normally bioturbated fine sand at stations 0·5 km to the west of Mannin Rocks. As the waves approach the platform they pass into shallower water. This results in an increase in velocity of the oscillating water currents and they frequently transport the gravel into wave ripples (λ100 cm, H 20 cm). A belt of rippled gravel is seen (text-fig. 7) on the edge of the platform.

When the waves pass over the platform their power to transport sediment is altered by two factors. Firstly, the sediment-transport potential of the waves, which are now shallow-water waves, is reduced by friction on the bottom. This is caused by primary porosity, bed forms, and grain size (Putnam and Johnson 1949). This I interpret as the cause of the loss of wave ripples as waves travel shorewards over the platform (text-fig. 7). The second factor to affect the power of the waves is caused by changes in topography of the bottom, leading to wave refraction. When wave orthogonals converge, at islands and submarine ridges, the wave energy increases. This I take to explain the wave ripples around Mannin Rocks, the shallow ridge extending shorewards from the rocks, and also the ripples to the south-west of Ardillaun (text-figs. 7 and 1). When wave orthogonals in embayments diverge, this results in a dissipation of energy and there are no wave ripples.

From the above, the Mannin platform can be divided into two hydraulic regions; one where waves are effective in moving bottom sediment and one where they are ineffective (text-fig. 7).

Text-figs. 6 and 7 show the presence and orientation of ripples and the distribution of the living maerl species. There is a marked negative correlation between these two parameters. Eighty-two per cent of those stations with more than 50% maerl do not have ripples. This suggests an inverse relationship between the oscillating bottom currents and the algal thallus and this is supported by observations made whilst diving that the growing apical tips are abraded when the algae are rolled on the sea-bed (Pl. 53, fig. 15). Thus the currents are possibly prohibiting growth.

Conclusions

From the above discussion it can be seen that there is an over-all depth restriction on the algae. I believe this to be primarily due to the light penetration of the bay waters. The only two parameters which vary with depth are temperature and light. The variation in temperature is very small (2 °C. over 20 m) in the bay due to its well-circulated waters. The summer temperatures recorded within the whole of the bay correspond to those given for maximum growth rates by Adey and McKibbin (1970). Light is therefore the only parameter which varies significantly with depth and it is therefore considered to be primarily responsible for the depth distribution of the maerl species in Mannin Bay.
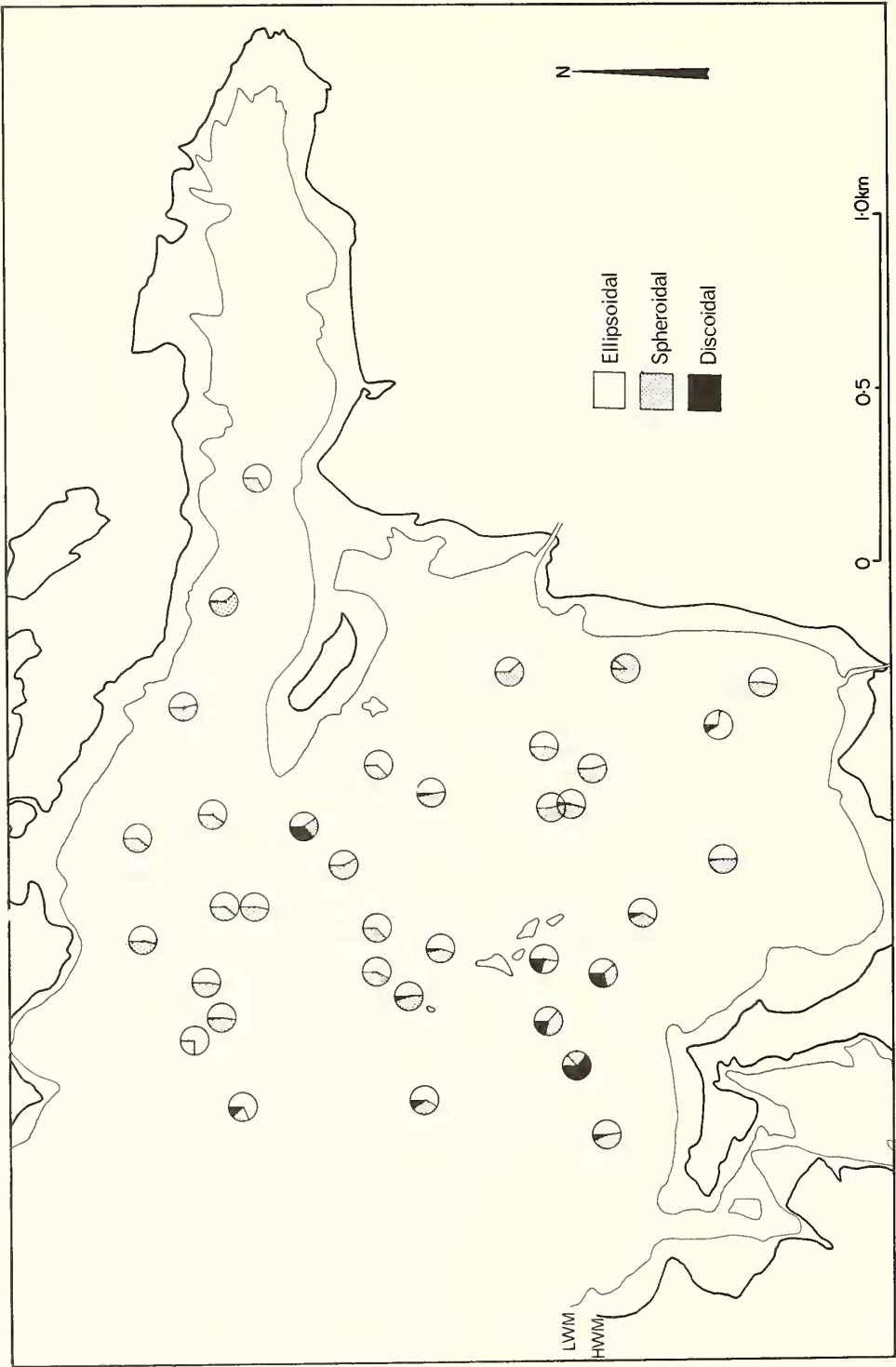
Within this depth range the distribution is limited in two ways. Firstly, in sheltered quiet creeks the algae are buried by mud which is stabilized by epiphytic filamentous
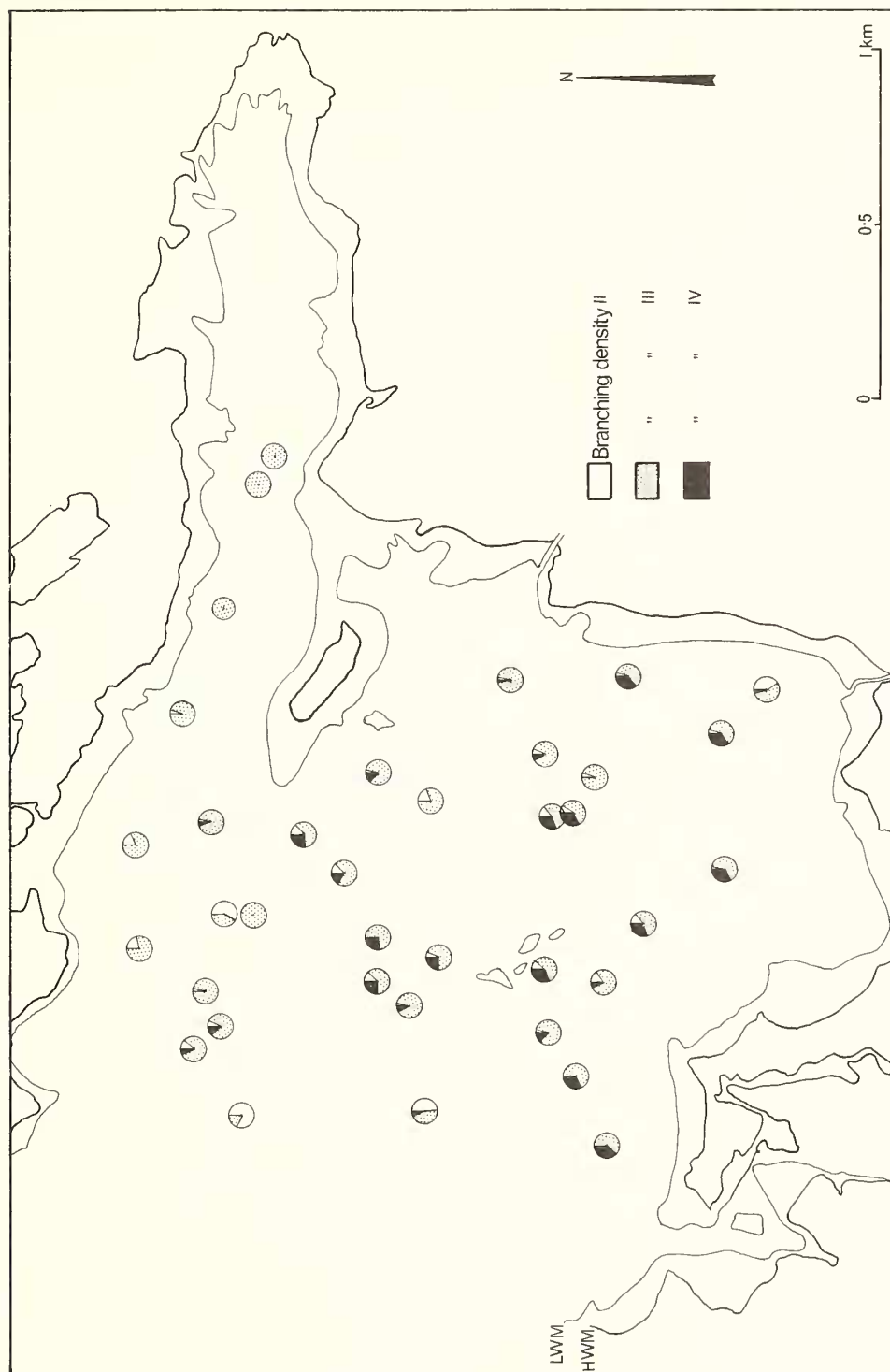
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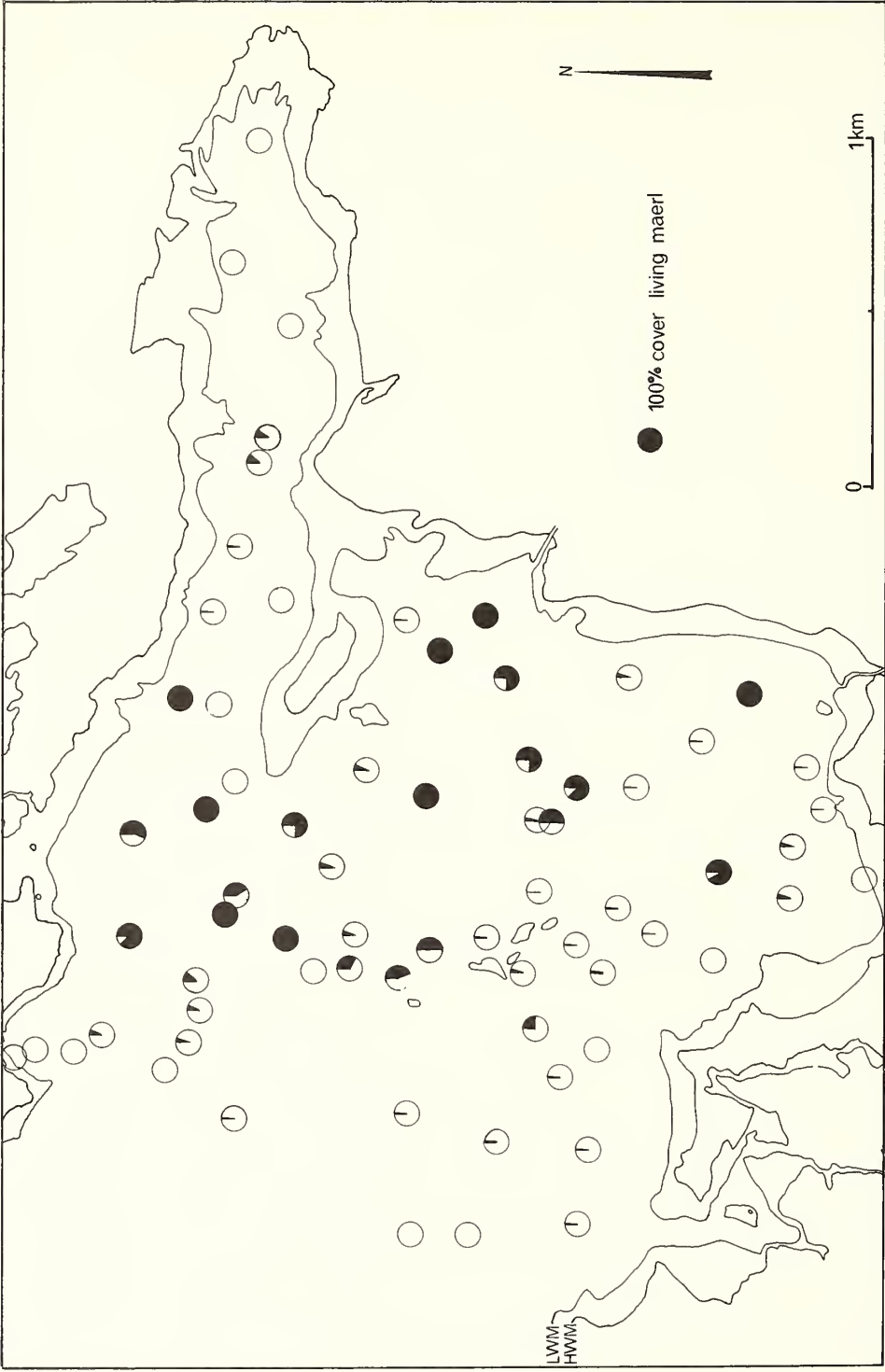
TEXT-FIG. 6. Distribution of living maerl as estimated from 50×50 cm quadrats.
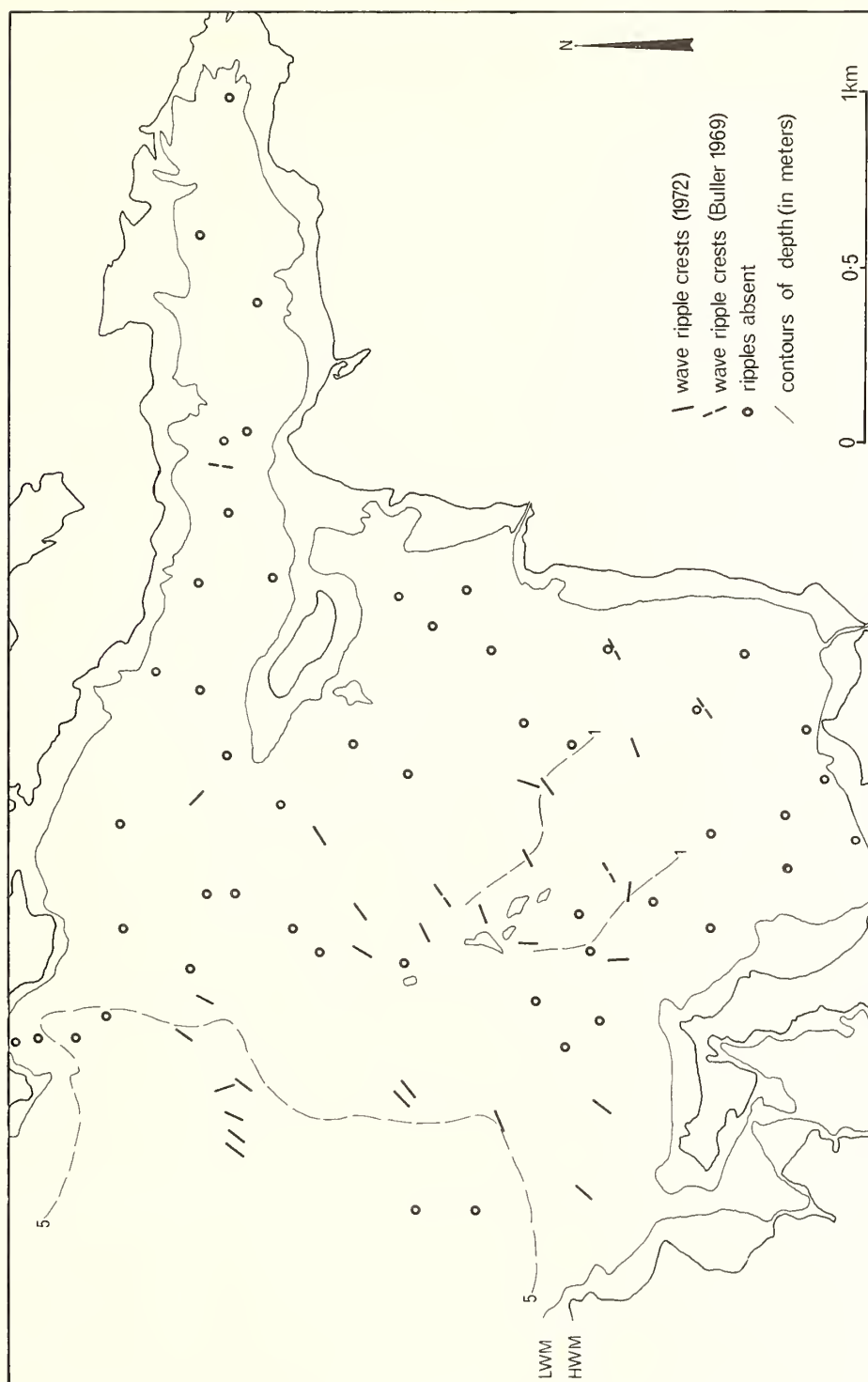
TEXT-FIG. 7. Distribution and orientation of wave ripples in *Lithothamnium* facies, Mannin Bay.

TEXT-FIG. 8. Distribution of shape classes of thalli of *Lithothamnium corallioides*, Mannin Bay.

TEXT-FIG. 9. Distribution of branching density of classes of thalli of *Lithothamnium corallioides*, Mannin Bay.

algae. Secondly, growth is controlled by the action of wave currents. This agrees with the conclusions of Adey and Adey 1973.

In Mannin Bay, *L. corallioides* is the dominant free-living calcareous alga, *P. calcareum* occurs as a smaller percentage of the total cover and at fewer stations. The relative abundance of these two species appears to be controlled by bottom currents. Whereas *L. corallioides* is ubiquitous but with more luxuriant growth in quieter waters *P. calcareum* occurs only in those areas of the bay where there are no ripples.

ANALYSIS AND DISTRIBUTION OF GROWTH FORMS

Variation of growth form

Both the maerl species show a parallel series of growth forms (text-fig. 10). This variation was first noticed and recorded by Foslie in 1894 and later by other authors including a detailed study by Cabioch (1966 and refs.). The growth forms shown in Plate 53, figs. 3–14 and text-fig. 10 illustrate those described by Cabioch and they are a continually varying morphological sequence. The value of the morphological groups is that they allow a fairly rapid and reproducible description of the varieties found. The nature and variability of the branching preclude the use of a relatively quick and accurate numerical analysis (but see below). However, one of the drawbacks is the use of form names to describe the variation in different species. If the same complex variation is found in other free-living corallines, as is apparent from the work of Bosellini and Ginsburg (1971) and Wray (1972), the use of separate form names for each variant of each species will add a large amount of new nomenclature into a subject which already has numerous taxonomic problems (for example, see Cabioch 1966). In addition to this Cabioch's method does not fully describe the variation of the discoidal forms (*compressa* and *flabelligera*).

An alternative scheme is suggested for describing the variation found in the free-living corallines which incorporates the systems of Cabioch (1966) and Bosellini and Ginsburg (1971) by relating forms to shape and branching density classes. Three shape classes can be recognized: spheroidal, ellipsoidal, and discoidal. These may be quantified using the method of Sneed and Folk (1958) for describing pebble shape. The three shape classes (see below, p. 386) may be related to environmental

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Fig. 1. Longitudinal section of *Lithothamnium corallioides* illustrating growth layers and dichotomous branching (acetate peel), ×60.

Fig. 2. Longitudinal section of *Lithothamnium corallioides* illustrating intercalary branching (acetate peel), ×60.

Figs. 3–4. Stereopair *Lithothamnium corallioides* spheroidal II, ×2.

Figs. 5–6. Stereopair *Lithothamnium corallioides* spheroidal IV, ×2.

Figs. 7–8. Stereopair *Lithothamnium corallioides* ellipsoidal II, ×1·5.

Figs. 9–10. Stereopair *Lithothamnium corallioides* ellipsoidal IV, ×1·5

Figs. 11–12. Stereopair *Lithothamnium corallioides* discoidal II, ×2.

Figs. 13–14. Stereopair *Lithothamnium corallioides* discoidal IV, ×2.

Fig. 15. *Lithothamnium corallioides* showing healing over of previously dead apices, ×3.

Fig. 16. Longitudinal section of *Lithothamnium corallioides* illustrating regeneration of secondary hypothallus and perithallus over old abraded apex (SEM micrograph), ×114.
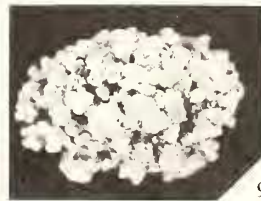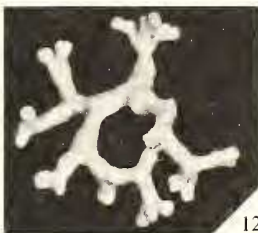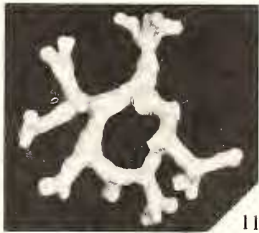
PLATE 53

BOSENCE, coralline algae
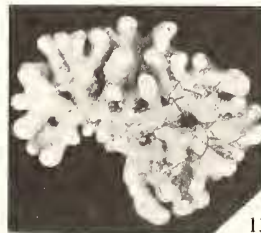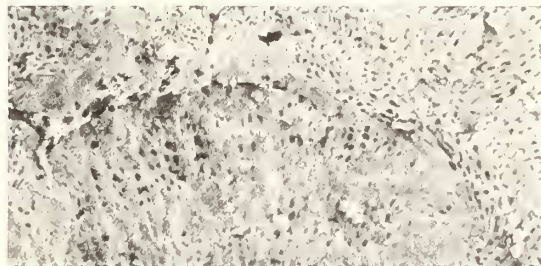
parameters. Within these shape classes four groups of relative density of branching can be seen: (i) one single main branch, (ii) few branches, (iii) frequent branching, and (iv) dense and solid intergrown thallus (nodule or rhodolith). This may be quantified by dividing the volume (taking as the volume of an ellipsoid with the same long, intermediate, and short axes) into the dry weight.

For very simple and young thalli the designation of shape class may be difficult but the system allows all the growth forms to be expressed in a practical and simple way, e.g. *L. corallioides spheroidal II* (text-fig. 10). Stereopairs of the three shape classes and branching density classes are on Plate 53, figs. 3–14.
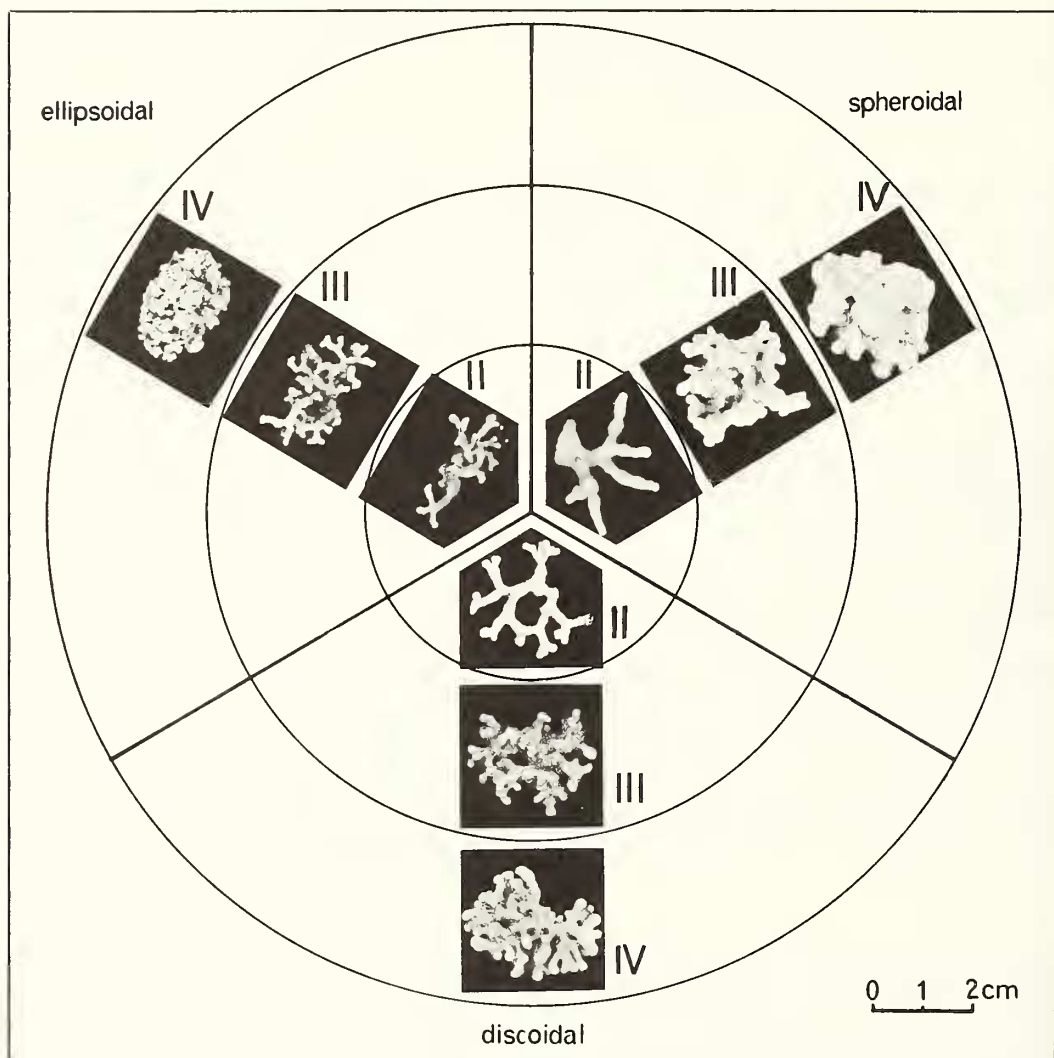
TEXT-FIG. 10. Diagram illustrating proposed classification of growth forms. Three shape classes are recognized: ellipsoidal, spheroidal, and discoidal. Within these shapes branching density varies from open branching (II) through frequent branching (III) to densely branched forms (IV).

The following list shows the relation between Cabioch's form names and the classification proposed here:

L. corallioides f. subsimplex	ellipsoidal I
L. corallioides f. subvalida	ellipsoidal II
L. corallioides f. australis	ellipsoidal III
L. corallioides f. corallioides	spheroidal III
L. corallioides f. globosa	spheroidal IV
L. corallioides f. flabelligera	discoidal III

An examination of the microstructure of the thallus was undertaken to investigate the nature of the branching. Cleaned specimens were embedded in a low-viscosity Araldite resin under vacuum and then longitudinal sections were ground through the branches and examined by taking acetate peels. An analysis of specimens of *L. corallioides* shows a close correlation between branching type and branching density:

	Branching type		
	Dichtomous	Intercalary	Uncertain
Branching density			
II and III (n = 28)	25 (90%)	none	3 (10%)
IV (n = 44)	17 (38·6%)	19 (43·2%)	8 (18·2%)

Therefore, whilst open branched forms (II and III) are characterized by dichotomous branching, densely branched forms are mainly formed by intercalary branching.

Distribution of growth forms

Lithothamnium corallioides. Text-figs. 8 and 9 show the distribution of thallus shape and branching density respectively. The commonest shapes for *L. corallioides* are spheroidal and ellipsoidal but these two growth forms show no obvious pattern of distribution. However, discoidal forms show a concentration in the southern part of the bay. The substrate in this area is a moderately well to poorly sorted fine to coarse sand (text-fig. 3) in contrast to the poorly sorted coarse algal substrate of the rest of the platform. The distribution of the branching density types illustrates a close correlation with exposure to wave-induced currents as shown by the presence of ripple marks (text-fig. 7). Seventy-two per cent of stations with more than 5% branching density IV are rippled. This is also noted from observations made whilst diving that the densely branched forms are found growing in the ripple troughs.

Phymatolithon calcareum. Ellipsoidal and spheroidal growth forms are again commonest as is branching density III but because of the limited distribution of the species no obvious patterns of distribution can be seen. The data has not, therefore, been presented.

Conclusions

The variation in growth forms in Mannin Bay indicates that the branching of the thallus increases with increasing exposure. This complements the work of Bosellini and Ginsburg (1971) and possibly Wray (1972). A discussion of the possible relationship between growth form and exposure must include an investigation into the hydrodynamics of the thallus. In particular the effect branching density has on the velocity for transport of the plants as this appears to be related to exposure.

THE HYDRODYNAMICS OF *LITHOTHAMNIUM CORALLIOIDES*

Experiments were designed to investigate the effect of thallus shape and branching density on the velocity for transport by wave-induced oscillatory currents.

Cleaned specimens of *L. corallioides* were selected to represent the range of shapes and branching densities found in Mannin Bay (Table 1; text-fig. 11); each shape class having nine specimens chosen to be as close as possible the same size. This was measured as the volume of an ellipsoid enveloping the thallus with the same long, intermediate, and short axes (Table 1). Branching density was quantified (see above, p. 382), II having an average density of 0·21, III 0·37, and IV 0·97 gm/cc (Table 1).
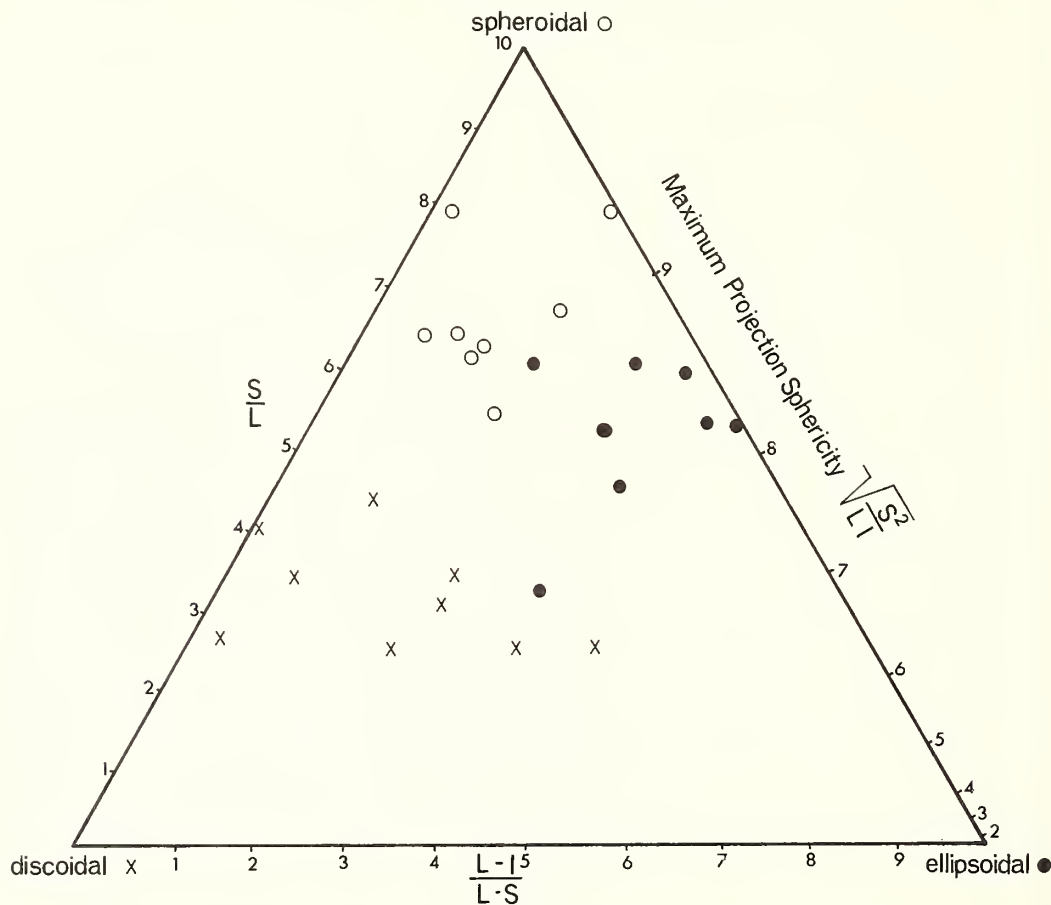
TEXT-FIG. 11. Sphericity-form diagram (after Sneed and Folk 1958) with experimental specimens plotted as independent fields of spheroidal, ellipsoidal, and discoidal shape classes.

Methods

Because of the many variables involved in the entrainment of particles by bottom currents, shape and density included, it was necessary to eliminate as many irrelevant factors as possible. The same substrate was used for all of the experiments; a single layer of medium-grained sand stuck on to a metal plate which was then placed on the floor of the tank. This was designed to be rough enough to restrict sliding of the

TABLE 1. Measurements and results of wave-tank studies for *Lithothamnium corallioides*. (Nos. 1–9 spheroidal forms, 10–18 discoidal forms, and 19–27 ellipsoidal forms. A1–4 and B1–4 models.)

Specimen no.	Volume cc	Weight gm	Density gm/cc	Velocity for transport Mean	Standard deviation
1	1·16	1·14	0·98	10·2	
2	1·00	0·37	0·37	12·4	3·6
3	0·46	0·08	0·17	11·4	1·3
4	0·84	0·61	0·73	9·8	
5	0·88	0·26	0·30	11·5	1·22
6	0·75	0·13	0·17	12·2	0·23
7	1·09	0·87	0·80	12·1	
8	1·53	0·38	0·25	11·5	1·02
9	1·30	0·14	0·11	12·0	2·13
10	0·71	0·63	0·88	12·6	
11	0·77	0·50	0·67	12·3	
12	0·76	0·26	0·34	18·9	
13	2·41	1·75	0·73	23·9	
14	1·41	0·59	0·42	16·2	3·1
15	1·32	0·21	0·16	11·0	
16	1·15	0·60	0·52	11·0	
17	1·65	0·83	0·51	26·4	
18	0·49	0·22	0·45	17·5	
19	2·07	1·72	0·83	9·1	0·29
20	1·56	0·50	0·32	8·3	0·73
21	2·30	0·54	0·23	8·3	0·73
22	2·45	2·37	0·97	8·2	
23	1·54	0·58	0·38	7·9	0·69
24	2·31	0·34	0·12	10·1	2·75
25	2·73	1·85	0·68	9·4	1·3
26	2·30	0·47	0·20	10·0	1·42
27	2·21	0·36	0·16	11·1	0·60
A1	14·1	1·06	0·07	19·2	0·64
A2	14·1	1·76	0·12	13·9	0·81
A3	14·1	2·30	0·16	12·4	0·72
A4	14·1	4·78	0·33	11·1	0·81
B1	14·1	1·16	0·08	15·1	1·69
B2	14·1	1·47	0·10	14·5	2·0
B3	14·1	2·26	0·16	11·4	1·15
B4	14·1	3·70	0·26	9·5	0·29

algae along the bottom (a mode of transport which has not been observed to occur in nature) but not rough enough to create turbulence which might interfere with the entrainment of the specimens. This was checked by observing the oscillation of fine particles in the water. Observations in Mannin Bay with dyes show that the waves produce currents around the thallus with an orbital motion with a slight shoreward drift. These conditions were obtained in the tank.

The wave tank used is at the Hydraulic Laboratory, Department of Civil Engineering, Imperial College, London. (Dimensions: 40 cm deep, 30 cm wide, and *c.* 6 m long.) Waves are generated by the vertical oscillation of a wedge-shaped piston against one end of the tank so that waves are only produced in one direction. The waves produced were varied in two ways: (*a*) by draining or filling the tank for variation of water depth, and (*b*) by varying the motor speed which drives the piston, this varies the wave height and celerity. The progressive waves so produced are absorbed by an artificial beach at the opposite end of the

tank. For each of three runs of the experiments a specimen was placed on the substrate in varying positions and the motor speed increased until the specimen was transported by the oscillating currents. When transport occurred the amplitude and celerity of the waves was measured.

Because the values for transport are only relative and not comparable with those in nature (this is due to the density difference of the water and the algae not having their coating of uncalcified cells and mucilage) the true near-bed velocity was not required for these experiments. Therefore the relative velocities were obtained by measuring depth (d), celerity (c), and amplitude (A) of the waves and from wave theory for shallow-water waves the maximum velocity is obtained from $U_{max} = cA/d$.

There were two main stages to the experiments. Firstly, qualitative observations were required on how transport occurred in the varying growth forms and what the controlling factors were in terms of the shape of the algal thallus. These were recorded on 16-mm film. The second stage was quantitative and designed to establish the relative velocities for transport of the various shapes and branching densities of the thallus to compare with their known distribution in Mannin Bay.

Qualitative observations

Spheroidal forms. The initial motion of the thallus with increasing current is determined by the support of the thallus on its branches which form a three- or four-point base. If these points are far apart (typical of open branched forms) a specimen will be more stable than one with the points closer together (typical of a densely branched form). This is because the centre of gravity of the thallus of the former will be lower and therefore the thallus will have to be pivoted higher to become unstable and brought into motion by the current. In addition, for a given volume the denser branched forms are perched higher than the open forms and this exposes them to the higher current values found away from the boundary layer. Associated with this is the observation that less densely branched forms appear to require greater velocities for transport than the more dense forms. This may be partly due to the increased surface area presented to the current and partly because the densely branched forms are less stable. The increased weight of these dense forms does not appear to be significant. The detail of the shape and pattern of branches on individual thalli can be seen to be very important in the initial rolling prior to transport.

Ellipsoidal forms. In addition to the points mentioned above which apply to all the growth forms, ellipsoidal forms appear to be transported at lower current velocities than spheroidal forms and at even lower velocities when placed with the long axis parallel to the wave crest than when placed normal to the wave crest. This would appear to be due to the increased surface area presented to the current.

Discoidal forms. These as would be expected from their shape, require greater velocities than both spheroidal and ellipsoidal forms for transport to occur. Those specimens which were slightly elongate orientate themselves with the long axis normal to the wave crest during motion.

Quantitative experiments

Each of the twenty-seven specimens (Table 1) was placed in three or sometimes two positions in the tank and the wave properties measured when the specimens were transported. This was defined as consistent turning induced by both forward- and backward-oscillating currents and a slight shoreward movement. The results are

shown in text-fig. 12. They confirm that ellipsoidal forms are more easily transported than spheroidal forms and that discoidal forms are the most stable (cf. Sneed and Folk 1958). Also the graphs for spheroidal and ellipsoidal forms suggest a slight negative correlation (not statistically significant) between branching density and current speed for transport, indicating that the open branched forms may be the most stable.
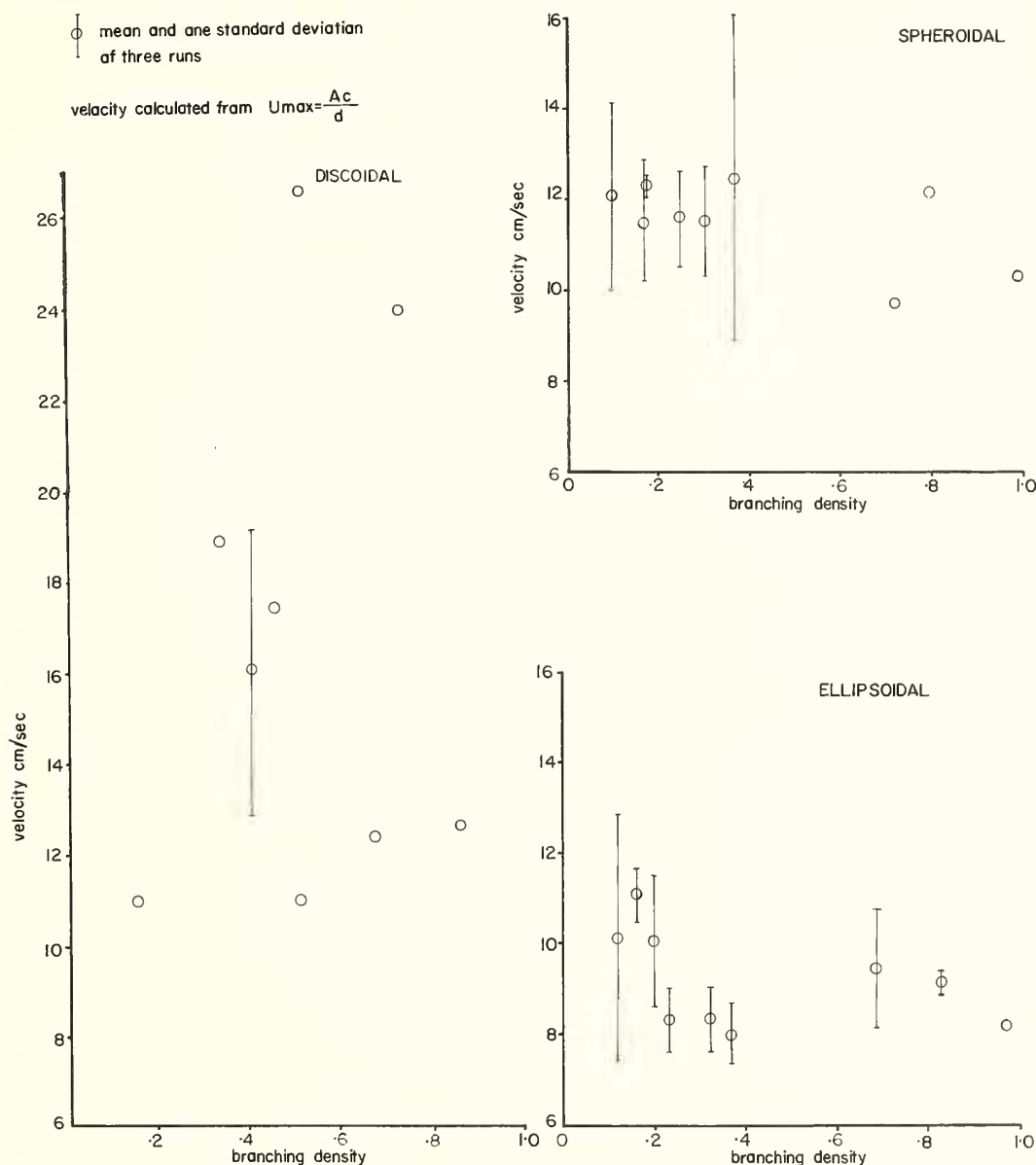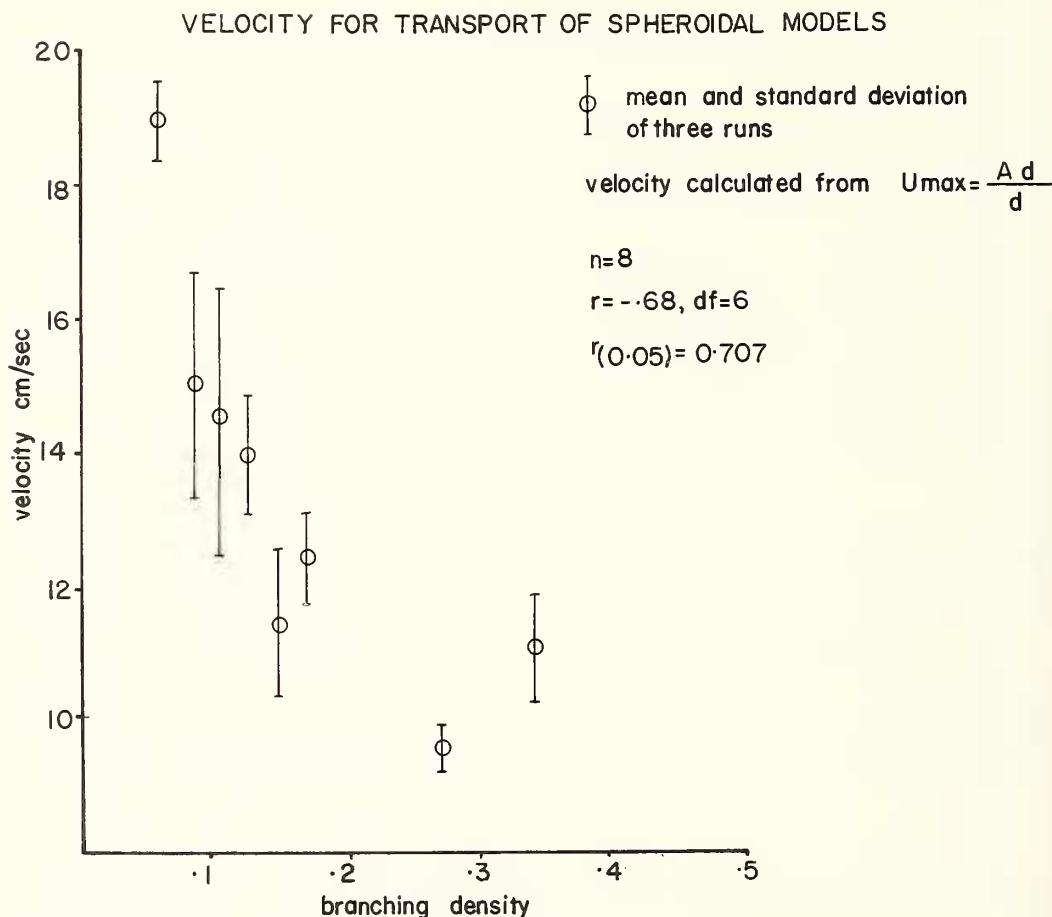

TEXT-FIG. 12. Graphs showing relationship between velocity for transport and branching density for *Lithothamnium corallioides*.

Discussion

The graphs illustrating the relationship between transport and branching density have plots which have a wider scatter. Close examination of individual specimens used indicates the unique shape of each specimen and a possible reason for its hydrodynamic behaviour. Small differences such as one slightly flattened surface are important in determining the velocity for transport. Therefore it is not always certain that one parameter of the thallus, such as branching density is always being compared, when other parameters such as size and shape are changing. There is a limitation in the material and exact replicates cannot be obtained (Table 1).

To ascertain whether branching density was more important than size and weight in limiting entrainment two series of models were constructed from plasticene which were the same size and shape (they were all spheres with the same diameter of 3 cm). The weights and branching densities of the models are shown in Table 1.

Text-fig. 13 shows the relationship between branching density and velocity of

TEXT-FIG. 13. Graph showing relation between velocity for transport and branching density for models of the maerl species.

transport and it indicates that an increase in branching density correlates with decreasing velocity for transport. The volume and shape of the models is the same but since the weight increases the branching density is the overriding factor. In conclusion, the densely branched forms are the most easily transported.

PREVIOUS WORK AND DISCUSSION

Previous work

It has been known for a long time that the Corallinaceae show great variation in growth form within one species (Johnson 1961, 1962; Cabioch 1966; Adey and Adey 1973) but this has only rarely been examined in the fossil record. This is partly due to the preoccupation with thallus microstructure and systematics by workers on ancient algae and, possibly, partly due to the fact that the studies made on specific variation in recent corallines have never been detailed and they lack any functional interpretation. To map or just record a correlation between growth form and an ecological factor does not prove that they are related but it leads to further detailed study and experiments.

Previous work on the distribution of growth forms of the free-living coralline algae is by Foslie (1894); Lemoine (1910); Jacquotte (1962); Cabioch (1966, 1969); Wray (1972); Bosellini and Ginsburg (1971); Adey and MacIntyre (1973); Adey and Adey (1973); Adey and McKibbin (1970).

Lemoine (1910) plotted the distribution of growth forms of *P. calcareum* form *squarrulosa* (= ellipsoidal III) and *crassa* (= spheroidal IV) for an area of southern Brittany. Form *squarrulosa* is found throughout the Isles de Brehat between depths of 4–18 m and in the outer regions of the Baie de Concarneau at depths of 10–15 m. This form is often found on muddy substrates where there is little current activity. She concludes that this ramifying form is adapted to life in a muddy environment. Form *crassa* is found in slightly shallower waters (3–15 m) to the north of the Isles de Brehat and south of the islands in the mouth of the Baie de Concarneau. She quotes from Foslie (1894) that the ball-like forms grow under the influence of strong currents.

Jacquotte (1962) working in the Mediterranean near Marseilles (Isles de Riou), studied the distribution of the two maerl species by diving, submersible, and drag sampling and found that *L. corallioides* was found on the upper part of a submarine slope on a clean gravel whereas *P. calcareum* was found at the deeper end of the slope on a muddy substrate. No variation of growth forms was noted.

Following Cabioch's (1966) systematic description of the growth forms of the maerl species she published (1969) a study on the beds of the Baie de Morlaix and concluded that the growth forms described were characteristic of different substrates (dredged samples). A coarse shell sand as found at Pighet, Terenez, and Primel contains all forms of *L. corallioides* var. *corallioides* (at Primel only *globosa* (spheroidal IV) is found), and with *P. calcareum* forms *calcarea* (ellipsoidal III), *squarrulosa* (spheroidal III), and *compressa* (discoidal III) are present. In contrast, a fine sand and mud substrate supports *L. corallioides* var. *minima* (not found in Mannin Bay). No information is given to explain the distribution of the growth forms or the two maerl species.

Bosellini and Ginsburg (1971) describe in detail the formation of rhodoliths from

free-living coralline algae, e.g. *L. occidental* in Bermuda. The branching forms (spheroidal and ellipsoidal III and IV) grow in the relatively sheltered *Thallasia testudinum* beds and may be transported out of the beds into adjacent sand-floored channels where they are frequently turned. The apices of the branches grow laterally, in response to abrasion, and fuse with adjacent branches to form a laminar coating. Subsequent laminae of the same or different species of encrusting corallines produces a rhodolith.

Recently Wray (*in* Ginsburg *et al.* 1972) illustrated a hypothetical coralline alga showing an increase in branching density and thickness of branches from deep to shallow water. No evidence is given to support the illustration and the change is not explained in terms of the many physical and chemical factors which vary with depth.

The work of Adey and authors (op. cit.) contains general statements on the variation of growth form in the unattached corallines and emphasizes the need for further work in this field.

Distribution of the maerl species in Mannin Bay

Observations in Mannin Bay confirm the work of Jacquotte (1962) who showed that *P. calcareum* grows in hydrodynamically quieter areas than *L. corallioides*. This may be due to the fact that the thallus of *P. calcareum* being the larger of the two species would extend further away from the lower velocity boundary layer and into faster-flowing water which would make it easier to transport than the smaller thallus of *L. corallioides*. The work of Cabioch (1969), however, suggests another interpretation. Long-term observations (1897–1964) in the Baie de Morlaix show that the proportions of the two species has varied over time. Sometimes this change is related to a change in the sediment of the area but at other times the relative proportions of the two species has been interpreted to be due to the very infrequent reproduction by spores (up to 6 years) which is then followed by an increase for that species. Therefore, the relative abundance and distribution of these two species may be due to spore-bearing periods rather than a direct environmental factor. Adey (1973) has shown that spore production is related to low water temperatures in a crustose coralline.

Distribution of shape classes in Mannin Bay

The variation of thallus shape has not been explained by previous workers. In Mannin Bay the origin of the discoidal forms can be interpreted as a response to a moderately to poorly sorted sand substrate in a relatively strong current area. A thallus living on sand will be prevented from growing downwards into the sand by the lack of light and will therefore grow upwards and laterally. If the thallus is frequently turned only lateral growths will be possible. In the coarse maerl this will not apply as the thallus is well supported by its neighbours.

The spheroidal and ellipsoidal forms do not appear to be related to any regional environmental parameters and the development of either of these forms must involve the detail of its position with respect to the substrate and its nearest neighbours throughout its life. Shape will also be affected by breakage during transport and biological activity.

Distribution of branching density classes in Mannin Bay

Comparing the results from the wave-tank studies with the distribution of forms with different branching density in Mannin Bay (text-fig. 9) shows that the open branched forms are found in the quiet areas and the dense forms in the exposed areas. The most stable form is therefore found in the quiet areas whereas the most unstable form is found in the most exposed areas. This may be explained as follows: when the thallus is rolled the apical tips of the branches are observed (Pl. 53, fig. 15) to be abraded and perhaps broken, further growth is restricted from these apical meristems. If abrasion is not prolonged the apex may heal from lateral undamaged cells growing over the tip (Pl. 53, fig. 16). However, if abrasion continues, growth may occur by resumption of previously dormant cells to produce an intercalary meristem within the protection of the main branches. This process will lead to an increase in branching density and also to a stronger form, because the branches may join, which will resist breakage but will also be more easily entrained.

This ties in well with the relative proportions of the dichotomous branching and intercalary branching (above, p. 383) found in the different growth forms; the densely branched forms having intercalary branching and the open branched forms dichotomous branching. The frequency of intercalary branching in the dense forms would indicate that the dense forms are a passive response by the alga to wave motion.

To test this, experiments could be designed involving the removal of specimens from one environment to another and noting any possible change in growth form. However, the longevity of the plants (*c.* 10 years) precludes this approach.

PALAEONTOLOGICAL IMPLICATIONS AND COMPARISONS

Autochthonous carbonate facies are sometimes used as indicators of tropical or subtropical climates in ancient sediments. This paper describes a regional autochthonous carbonate facies from a cool temperate climatic belt. The banks occur in an area of regional biogenic carbonate deposition which is probably forming because of the lack of dilution by terrigenous clastics. The banks are restricted to depths of between 1 and 18 m and to relatively unexposed parts of the bay. Locally the banks are broken down to form an algal gravel.

The analysis of phenotypic variation in *L. corallioides* is based on mapping, thallus structure, and experimental work. Two sequences of variation are found which would enable palaeontologists to (*a*) make detailed interpretation of the palaeoenvironment, and (*b*) to beware of using these characters for taxonomic purposes. Shape is found to vary with substrate and possibly with exposure. Discoidal forms develop on an exposed medium–fine grained substrate whereas ellipsoidal forms grow on a coarse gravel substrate in quiet and exposed areas. Increase in branching density and lateral, as opposed to dichtomous, branching both increase with exposure to bottom currents.

The algal banks recorded in Mannin Bay are very similar in structure to the *Goniolithon* banks described by Turmel and Swanson (1972) and Ginsburg and James (1974) from Florida. Major differences are that these subtropical banks are zoned (e.g. Rodriguez Bank) and the free-living *Goniolithon* forms only one zone on the windward margin of the bank. The associated fauna and flora appears at first sight to be equally diverse in both temperate and subtropical banks but to confirm this

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detailed studies are still required from both areas. When deciding whether ancient banks are temperate or tropical the associated skeletal fauna and flora will be conclusive. The temperate banks lack corals (*Porites porites*) and the calcified Chlorophycean algae (*Halimeda, Penicillus, Rhipocephalus*). The distinction between the petrography and geochemistry of temperate and tropical carbonates is discussed by Buller (1969), Gunatilaka (1972), Lees and Buller (1972).

As far as I am aware no analogous pre-Pleistocene algal facies have been described. The most similar Palaeozoic examples are the Pennsylvanian algal limestones described by Wray 1964, 1972, and Frost 1975. These banks are constructed by species of *Archaeolithophyllum* which have a platey thallus. The banks are always associated with soft substrate areas and are occasionally intercalated with cross-bedded skeletal debris. The main difference between these limestones and the algal banks described in this paper is the shape of the algal thallus. However, the construction of the bank and the relationship of the bank to the skeletal debris facies is similar.

Algal limestones produced by closely related genera are common in the Tertiary sediments of the Mediterranean and Pacific regions (Elliott 1959 and refs., 1970; Lemoine 1939; Mastorelli 1967; Johnson 1961, 1962, 1963; Pedley 1974). However, most of the work is concerned with the systematics of the algae and very little information is given apart from the detailed internal morphology of the thallus. The preservation and limestone petrography is rarely explained.

An exception to this is Pedley's (1974) study from Malta where algal limestones are found in the Oligocene Lower Coralline Limestone Formation (*Lithothamnium* sp. and *Archaeolithothamnium* sp.) and Miocene Upper Coralline Limestone Formation (*Lithophyllum* cf. *destefonii* Samsonoff). The limestones are formed on a broad shelf with a 27×6 km bioherm facies stretching north–south through Malta and Gozo.

The bioherms which are up to 16 m thick are established on a sharp-topped horizon of the Blue Clay Formation. The algal thalli are roughly elliptical in shape with diameters varying from 50 to 100 mm. They are partially micritized and are preserved in a micrite matrix. Mud deposition was relatively rapid as the bioherm is built of alternating layers of micrite and algae. The mud is thought to have been stabilized by marine grass. Surrounding the bioherms are beds composed of transported algal debris. Associated with the bioherms is an abundant fauna with representatives of the same ecological groups as those found in Mannin Bay with the addition of infaunal echinoids in the micrite interbeds.

In many respects these bioherms and algal debris facies are analogous to the recent deposits of the platform in Mannin Bay. However, the coral and foraminifera species indicate that the limestones were formed in a tropical to subtropical climate and they may turn out to have more in common with the *Goniolithon* banks of Florida Bay.

CONCLUSIONS

Algal sediments are forming within an area of regional temperate carbonate deposition with associated biogenic carbonate facies. The sea-water is normal marine with water temperatures varying from 5 °C. in winter to 15 °C. in summer.

The unattached corallines are found at depths from extreme low-water spring tides to 16 m. However, prolific growth is only found between depths of 1 and 8 m.

The algal sediments are composed of autochthonous algal banks surrounded by an algal debris facies. The growing banks have a positive relief of up to 30 cm and cover areas measured in thousands of square metres. They support a diverse fauna in comparison with the surrounding algal debris facies.

The distribution of the maerl species is discussed with respect to the salinity, pH, Eh, calcium and magnesium ion concentration, temperature, light, and exposure of the bay waters. It is concluded that there is an over-all depth restriction controlled by light penetration and within this zone growth is restricted by exposure to wave currents. The algal banks are therefore found in the quieter areas of the bay.

The life cycles, morphology, and mode of branching of the two corallines is described. Branching can occur in two ways. Either through apical dichotomy or by resumption of previously dormant cells to form a lateral branch.

The two species show a parallel series of phenotypic morphological variation. A scheme is suggested for describing the variation found in the free-living corallines. Three shape classes are recognized: spheroidal, ellipsoidal, and discoidal. Within each shape class four groups of relative density of branching can be seen. These vary from open branched forms through frequently branched thalli to closely branched solid thalli or rhodoliths.

A study of the microstructure of the thallus shows that open branched forms are characterized by dichotomous branching and densely branched forms by intercalary branching.

The distribution of the shape and branching density classes is mapped. The commonest shapes are spheroidal and ellipsoidal forms which show no obvious pattern of distribution. Discoidal forms, however, are found on fine- to medium-grained substrates in the relatively exposed parts of the bay. The distribution of the densely branched forms is found to be closely correlated with exposure to bottom currents.

A study is made of the hydrodynamics of the thallus of *Lithothamnium corallioides* using a wave tank. The results show that ellipsoidal forms are more easily transported than spheroidal forms and that discoidal forms are the most stable. The open branched forms are more stable than the densely branched forms.

From the analysis of the distribution and hydrodynamics of the growth forms of the two species their occurrence in Mannin Bay is discussed. Discoidal forms develop as a response to frequent turning on a fine- to medium-grained substrate where downward growth is prohibited. Spheroidal and ellipsoidal forms do not appear to be related to any regional environmental parameters. Branching density is positively correlated with exposure. Therefore, the most easily transported forms are found in the most exposed areas and the stable forms in the quieter areas. This is explained through the analysis of branching of the thallus; following apical abrasion after transport it is suggested that the thallus undergoes lateral branching. If this continues a densely branched solid thallus or rhodolith is formed. With little or no transport in the quieter areas of the bay, the thallus undergoes dichotomous branching.

The palaeontological implications of the work are discussed and comparisons made with recent subtropical algal banks, Tertiary algal banks, and Pennsylvanian algal banks.

REFERENCES

ADEY, W. H. 1966. Distribution of saxicolous crustose corallines in the north-western North Atlantic. *J. Phycol.* **2**, 49–54.

—— 1970. The effects of light and temperature on growth rates in boreal-subarctic crustose corallines. Ibid. **6**, 269–276.

—— 1973. Temperature control of reproduction and productivity in subarctic coralline algae. *Phycologia*, **2**, 2–20.

—— and ADEY, P. J. 1973. Studies on the biosystematics and ecology of the epilithic crustose Corallines of the British Isles. *Br. Phycol. J.* **8**, 343–407.

—— and MCKIBBIN, D. L. 1970. Studies on the maerl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnium corallioides* Crouan in the Ria de Vigo. *Botanica mar.* **13**, 100–106.

—— and MACINTYRE, I. G. 1973. Crustose coralline algae; a re-evaluation in the geological sciences. *Bull. geol. Soc. Am.* **84**, 883–903.

ALLEN, J. R. L. 1970. *Physical processes of sedimentation*. London. 248 pp.

BAGNOLD, R. A. 1947. Sand movement by waves; some small scale experiments with sand of very low density. *J. Inst. Civ. Eng.* **5554**, 447–469.

BARBER, R. F. 1965. *Water waves*. London. 180 pp.

BOSELLINI, A. and GINSBURG, R. N. 1971. Form and internal structure of recent algal nodules (Rhodolites), Bermuda. *J. Geol.* **79**, 669–682.

BULLER, A. T. 1969. Source and distribution of calcareous skeletal components in recent marine carbonate sediments, Mannin and Clifden Bays area, Connemara, Ireland. Unpubl. Ph.D. thesis, Reading University.

CABIOCH, J. 1966. Contribution à l'étude morphologique anatomique et systématique de deux Mélobésiées: *Lithothamnium calcareum* (Pallas) Areschoug et *Lithothamnium corallioides* Crouan. *Botanica mar.* **9**, 33–53.

—— 1969. Les fonds de maerl de la baie de Morlaix et leur peuplement végétal. *Cah. Biol. mar.* **10**, 139–161.

—— 1970. Le maerl des côtes de Bretagne et le problème de sa survie. *Penn ar Bed*, **7**, 421–429.

—— 1972. Étude sur les Corallinacées. II. La morphogenèse conséquences systématiques et phylogénétiques. *Cah. Biol. mar.* **13**, 137–288.

CABIOCH, L. 1968. Contribution à la connaissance des peuplements benthiques de la Manche occidental. Ibid. **9**, 493–711.

ELLIOTT, G. F. 1959. Fossil calcareous algal floras of the Middle East with a note on a calcareous problematicum *Hensonella cylindrica* gen. et sp. nov. *Q. Jl geol. Soc. Lond.* **115**, 217–232.

—— 1970. *Pseudaethesolithon*. A calcareous alga from the Fars (Persian Miocene). *Geol. Romana*, **9**, 31–46.

FOSLIE, M. 1894. The Norwegian forms of *Lithothamnion*. *D. Kgl. Norske Vidensk. Selsk. Skrift*, **2**, 1–203.

FROST, J. G. 1975. Winterset Algal-bank complex, Pennsylvanian Eastern Kansas. *Bull. Am. Ass. Petrol. Geol.* **59**, 265–291.

GINSBURG, R. N. and JAMES, N. P. 1974. Spectrum of reef building communities in the western Atlantic. *In* ZIEGLER, A. M. (ed.). *Principles of benthic community analysis.* Sedimenta IV, Comparative Laboratory of Sedimentology, Miami University. 165 pp.

GUNATILAKA, H. A. 1972. A survey of the geochemistry and diagenesis of recent carbonate sediments from Connemara, Western Eire. Unpubl. Ph.D. thesis, Reading University.

JACQUOTTE, R. 1962. Étude des fonds de maerl de la Méditerranée. *Recl. Trav. Stn. mar. Endoume*, **26**, 141–235.

JOHNSON, J. H. 1961. *Limestone-building algae and algal limestones.* Colorado School of Mines, 267 pp.

—— 1962. The algal genus *Lithothamnium* and its fossil representatives. *Colo. Sch. Mines Q.* **57**, 1–111.

—— 1963. The algal genus *Archaeolithothamnium* and its fossil representatives. *J. Paleont.* **37**, 175–211.

KEAGAN, B. 1973. Studies on the benthic communities and Bivalvia of Galway and Kilkieran Bays. Unpubl. Ph.D. thesis, University College, Galway, Eire.

KEARY, R. 1969. Variations in biogenic carbonate content of beaches on the south coast of Ireland. *Scient. Proc. R. Dubl. Soc.* Ser. A, **3**, 193–202.

—— 1970. Coastal climate and the shelf bottom sediments: a comment. *Mar. geol.* **8**, 363–365.

LEES, A., BULLER, A. T. and SCOTT, J. 1969. *Marine carbonate sedimentation processes, Connemara, Ireland.* University of Reading, Geology Dept. Report No. 2. 64 pp.

—— —— 1972. Modern temperate water and warm water shelf carbonate sediments contrasted. *Mar. geol.* **13**, M67–M73.

LEMOINE, P. 1910. Répartition et mode de vie du maerl (*Lithothamnium calcareum*) aux environs de Concarneau (Finistère). *Ann. Inst. Océanogr. Monaco*, **1**, 1–28.

—— 1939. Les algues calcares fossiles de L'Algerie. *Mater. Carte geol. Alger*, **1**, 9, 1–128.

MASTORELLI, V. I. 1967. Nuovo contributo allo studio delle corallinaceae dell'Oligocene Ligne-Piemontese: I Reparti delta favolette Pouzone. *Atti Ist. geol. Genova*, **5** (11), 153–390.

PEDLEY, M. 1974. Oligo–Miocene sediments of the Maltese Islands. Unpubl. Ph.D. thesis, Hull University.

PUTNAM, J. A. and JOHNSON, J. W. 1949. The dissipation of wave energy by bottom friction. *Trans. Am. Geophys. Union*, **30**, 67–74.

SCOTT, J. 1970. The nature and distribution of living and dead foraminiferida Clifden and Mannin Bays, County Galway, Eire. Unpubl. Ph.D. thesis, Reading University.

SNEED, E. D. and FOLK, R. L. 1958. Pebbles in the lower Colorado river Texas; Study in particle morphogenesis. *J. Geol.* **66**, 114–150.

TURMEL, R. and SWANSON, R. 1972. Rodriguez Bank. *In* GINSBURG, R. N. (ed.). *South Florida Carbonate Sediments.* Sedimenta II, Comparative Laboratory of Sedimentology, Miami University. 72 pp.

WRAY, J. L. 1964. *Archaeolithophyllum.* An abundant calcareous alga in limestones of the Lansing Group (Pennsylvanian) south east Kansas. *Kansas, geol. Survey, Bull.* **170**, 1–13.

—— 1972. Ecology and Geologic distribution. *In* GINSBURG, R. N., REZAK, R. and WRAY, J. L. *Geology of the calcareous algae.* Sedimenta I, Comparative Laboratory of Sedimentology, Miami University. 70 pp.

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